Efficiency of aggregations for shell recruitment by hermit crabs.

REDIA, LXXXVII, 2004: 235-237

ELENA TRICARICO (*) - JELLA ATEMA (**) - FRANCESCA GHERARDI (*)

EFFICIENCY OF AGGREGATIONS FOR SHELL RECRUITMENT BY HERMIT CRABS (DECAPODA ANOMURA)

(*) *Università di Firenze, Dipartimento di Biologia Animale e Genetica «Leo Pardi», Firenze, Italy, elena.tricarico@unifi.it*
(**) *Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts, USA*

Tricarico E., Atema J., Gherardi F. - Efficiency of aggregations for shell recruitment by hermit crabs (Decapoda Anomura)

Several species of hermit crabs form aggregations around gastropod predation sites. The literature suggests that these aggregations mainly function as «shell markets», being mostly attended by hermit crabs occupying badly fitting shells. In the summer 2004, we conducted experiments and observations in a salt marsh of New England (USA) to understand the relative role played by aggregations in *Pagurus longicarpus*' shell recruitment.

KEY WORDS: odour, shell recruitment, hermit crabs, *Pagurus longicarpus*

INTRODUCTION

Hermit crabs require empty gastropod shells to protect their soft abdomen. A high quality shell is an essential resource for them. In fact, the occupancy of badly fitting shells reduces individual fitness by negatively affecting fecundity, growth, and survivorship (SPIGITT, 1985).

Similarly to other species, the salt marsh hermit crab *Pagurus longicarpus* responds in an adaptive fashion to several chemical stimuli that signal shell availability (RITTSCHOF, 1980a; RITTSCHOF *et al.*, 1992). Odours released by the digested tissues of injured gastropods attract crabs, specifically small individuals occupying badly fitting shells (RITTSCHOF, 1980a,b). Their responses are selective. In fact, they are not attracted by flesh of crustaceans or bivalves (RITTSCHOF, 1980a). The attracted individuals form temporary aggregations around gastropod predation sites. The dominant crabs in the group usually occupy the empty shell in the site, and obviously release their previously inhabited shell that is made available to conspecifics. This first shell switch is usually followed by a cascade of shell exchanges between attendants (HAZLETT, 1978). As a consequence, aggregations seem to benefit several individuals in the group, therefore functioning as «shell markets» (RITTSCHOF *et al.*, 1992).

Our purpose here was to verify in *P. longicarpus* whether aggregations formed around a simulated predation site are really effective for the acquisition of new shells. To this end, we analysed this and other two potential strategies of shell recruitment in this species, i.e. exploration of the habitat and exploitation (independently of aggregations) of gastropod predation sites and of other possible sites of shell recruitment.

MATERIAL AND METHODS

The long-clawed hermit crab, *P. longicarpus* Say 1817, is common in shallow waters along the western Atlantic coasts of North America and in the northern Gulf of Mexico. In July 2004, we conducted experiments and observations in Little Sippewissett salt marsh (Massachusetts, USA) with the purpose of analysing three possible strategies for shell recruitment: exploration, exploitation, and aggregation.

First, to analyse the efficiency of exploration, 42 hermit crabs were tracked *in continuum* for 30 minutes in four different phases of diurnal tide cycles (high tide, HT; flood tide, HT-LT; low tide, LT; ebb tide, LT-HT). During our observations, we recorded: (1) the final distance measured from the starting point (D0); (2) the total distance covered (DT); (3) the number of encounters with other hermit crabs; (4) the number of encounters with empty shells of *Littorina littorea*, the snail most frequently used by *P. longicarpus*; and (5) the number of shell exchanges.

Second, to analyse the efficiency of exploitation, we followed in part RITTSCHOF's protocol (1980b) and simulated shell recruitment sites using experimental net bags (size: 10X20 cm, mash size: 2 mm) filled with crushed or live *L. littorea*, crushed or live conspecifics, and a stone as a control reaching a total of 60 replicates (12 per treatment). An empty *L. littorea* shell was placed in proximity of each bag. For an hour, we recorded latency time, the number of crabs attending the site, and the number of shell exchanges. These simulated shell recruitment sites were checked after 2 and 3 hours from the starting of the experiment.

Third, to analyse the efficiency of aggregation, we tied an empty shell with a nylon thread to a bag as above containing crushed *L. littorea* that simulated a gastropod predation site. The experimental shell had the aperture blocked by a resin to impede the occupancy by the crabs. During an hour of observation on a total of 10 aggregations, we recorded the number of crabs attending the site, the number and types of interactions, and the number of shell exchanges. Following in part GHERARDI & TIEDEMANN (2004), interactions were distinguished into: avoidances (i.e. one opponent retreated with no overt response by the other); threats (i.e. one opponent retreated when the other extended its chelipeds or raised its pereopods or flicked its antennae or chelipeds), weak contacts (i.e. one opponent retreated after the occurrence of antennal contacts or touches with chelipeds or pereopods), strong contacts (i.e. one opponent retreated after the occurrence of grasps or strikes), and events of shell rapping (a behavioral pattern associated with shell fights, HAZLETT, 1978).

Since the assumptions of normality of data and homogeneity of variance were not always met, we used non-parametric tests following the procedures found in SIEGEL & CASTELLAN (1988). Independent and related samples were

– Published September, 2005

compared with Kruskall-Wallis one-way analyses of variance (statistic H) and Friedman two-way analyses of variance (statistic F_r), followed by Multiple Comparisons tests, respectively. Spearman rank-order correlation (statistic r_s) was used for non parametric correlations. Text and figures give medians and interquartile ranges (first-third quartiles). The level of significance at which null hypothesis was rejected is $\alpha = 0.05$.

RESULTS

Exploration

DT was positively correlated with the number of the conspecifics that the tracked crabs encountered during their exploration (r_s=0.562, t=4.302, df=40, P<0.001) (fig. I, 1). At least one conspecific was encountered by 95% of the tracked crabs; however, we recorded only two events of shell rapping and no shell exchanges between crabs. DT was also positively correlated with the number of the encountered empty shells (r_s=0.53, t=3.95, df=8, P<0.001) (fig. I, 2). 52% of the tracked crabs found an empty shell, but the encountered shells were explored only by four individuals and were occupied by two. No correlation was found between the number of the encountered conspecifics or the number of the encountered empty shells and the accuracy of exploration, calculated as D0/DT (number of hermits: r_s=0.201, t=1.296, df=40, n.s.; number of empty shells: r_s=0.104, t=0.662, df=40, n.s.).

Exploitation

The time of arrival of the first crab at the recruitment site and the maximum number of crabs attending the site differed significantly across treatments (arrival time: H=29.04, df=4, P<0.001; maximum number: H=34.56, df=4, P<0.001), the bags containing crushed snails being more attractive (after Multiple Comparison test for both analysis: dead snails>live hermits=dead hermits>live snails=control) (figs II and III).

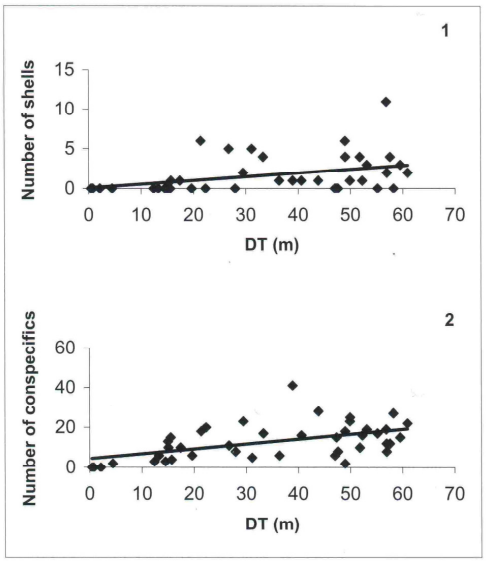

Fig. I – Relationships between the total distance covered (DT) and: (1) the number of shells and (2) the number of conspecifics encountered during exploration by the 42 tracked hermit crabs.

The experimental shell was acquired by a crab in 85% of cases (51/60). The lowest rate of acquisition was recorded with the control and the bags containing live snails. 88% of crabs occupying the experimental shell did not leave the formerly occupied shell in the site, but seized it with the major chela and took it away from the site. No shell exchanges between crabs were ever observed. The number of attendants decreased with time (fig. IV).

Aggregation

The number of crabs attending the site was always high and did not change during the hour of observation (F_r=2.69, df=5, n.s.). We recorded different types of interactions between crabs (F_r=18.10, df=4, P=0.0012), but the recorded aggressive level, as indicated by strong contacts and shell rapping, was low (after Multiple Comparison: threat>weak contacts>avoidance =strong contacts>shell rapping). We observed only 10 events of shell rapping on a total of 969 interactions (fig. V). No shell exchange between crabs was ever recorded.

DISCUSSION

Our objective was to analyse the relative efficiency of aggregations in *Pagurus longicarpus*' shell recruitment. We found that:

(1) The length of exploration, but not its accuracy, increased the probability of encountering both conspecifics and empty shells; however, shell exchanges were rare;

(2) Crushed snails, and to a lesser extent live and crushed conspecifics, attracted crabs; however, after having occupied the experimental shell, crabs usually seized the released shell and took it away from the site. As a consequence, only the first attendant to the site has the opportunity of getting benefit from the predation event. Previous studies have shown that *P. longicarpus* is inaccurate in distinguishing shells by sight (Gherardi & Tiedemann, 2004) and often switches shells without prior investigation (Scully, 1986). We therefore hypothesize that the decision of either to keep the novel shell or to return to the old one requires some proprioceptive information of «comfort» that the crab is able to acquire only by wearing it. To avoid loosing the previously occupied shell before knowing the effective quality of the novel one, crabs should cautiously subtract it from competitors. The disappearance of empty shells induces a quick decrease in the number of crabs attending the site, which cannot be explained by the reduced effect of the odor of crushed snails (simulated gastropod predation sites still attract crabs after 24 h; Rittschof, 1980a).

(3) Aggregations attract a large number of crabs for a relatively long time, but they do not function as «shell markets» as suggested by the literature; in fact, we did not observe any shell exchanges between crabs and the aggressive level was constantly low.

In essence, our results clearly show that *P. longicarpus* recruits new shells using different strategies than the other hermit crab species studied so far and demand additional studies to understand the proximate causes of this interspecific difference.

RIASSUNTO

EFFICIENZA DEL GRUPPO PER IL RECLUTAMENTO DI CONCHIGLIE NEI PAGURI (DECAPODA ANOMURA)

Molte specie di paguri formano aggregazioni sui siti di predazione dei gasteropodi. La letteratura afferma che queste aggregazioni funzionano da «mercati di scambio di

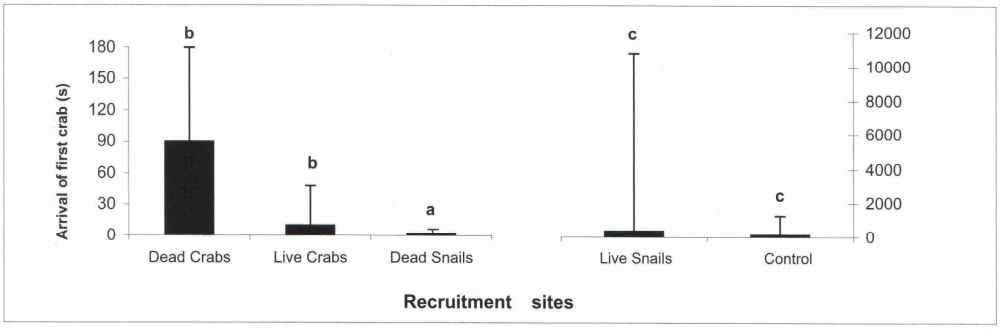

Fig. II – The time of arrival by the first attendant at the shell recruitment sites.

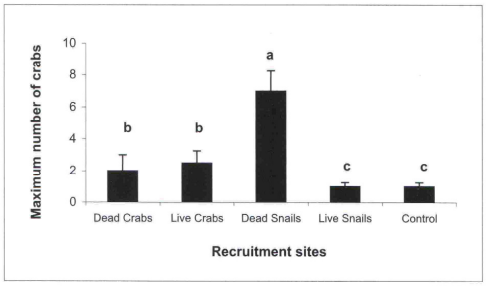

Fig. III – Maximum number of attendants to the different shell recruitment sites.

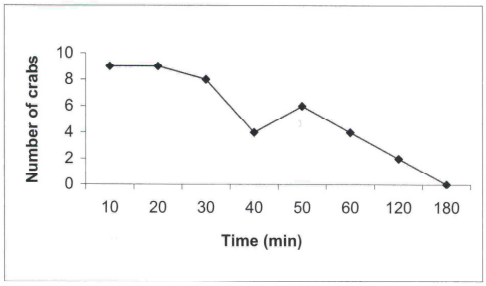

Fig. IV – Decrease with time of the number of hermit crabs attending the simulated gastropod predation sites.

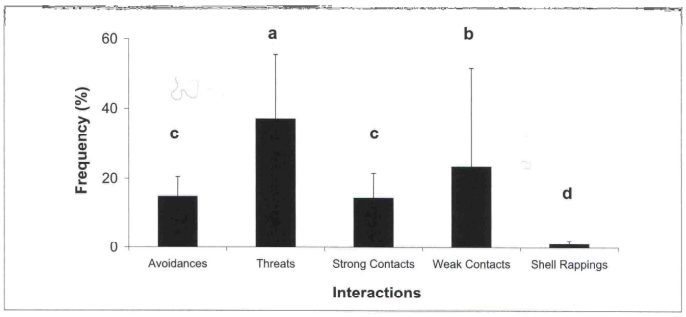

Fig. V – Frequency of the different types of interactions between hermit crabs.

conchiglie» e sono frequentate soprattutto da paguri che occupano conchiglie subottimali. Nell'estate del 2004, abbiamo condotto una serie di osservazioni ed esperimenti in un «salt marsh» del New England (USA) per individuare il ruolo che tali aggregazioni esercitano nel reclutamento di conchiglie da parte di *Pagurus longicarpus*.

REFERENCES

GHERARDI F., TIEDEMANN J., 2004 – *Binary individual recognition in hermit crabs.* - Behav. Ecol. Sociobiol., 55: 524–530.

HAZLETT B. A., 1978 – *Shell exchanges in hermit crabs: aggression, negotiation or both?* - Anim. Behav., 26: 1278–1279.

RITTSCHOF D., 1980a – *Chemical attraction of hermit crabs and other attendants to gastropod predation sites.* - J. Chem. Ecol., 6: 103–118.

RITTSCHOF D., 1980b – *Enzymatic production of small molecules attracting hermit crabs to simulated predation sites.* - J. Chem. Ecol., 6: 665–676.

RITTSCHOF D., TSAI D. W., MASSEY P. G., BLANCO L., KUEBER G. L. JR., HAAS R. J. JR., 1992 – *Chemical mediation of behavior in hermit crabs: alarm and aggregation cues.* - J. Chem. Ecol., 18: 959–984.

SCULLY E. P., 1986 – *Shell investigation behavior of the intertidal hermit crab* Pagurus longicarpus Say. - J. Crust. Biol., 6: 749-756.

SIEGEL S., CASTELLAN N. J. JR., 1988 – *Nonparametric statistics for the behavioral sciences.* - New York: McGraw-Hill, pp: 1-399.

SPIGHT T.N., 1985 – *Why small hermit crabs have large shells.* - Research in Population Ecology, 27: 39-54.